Biological Report 14
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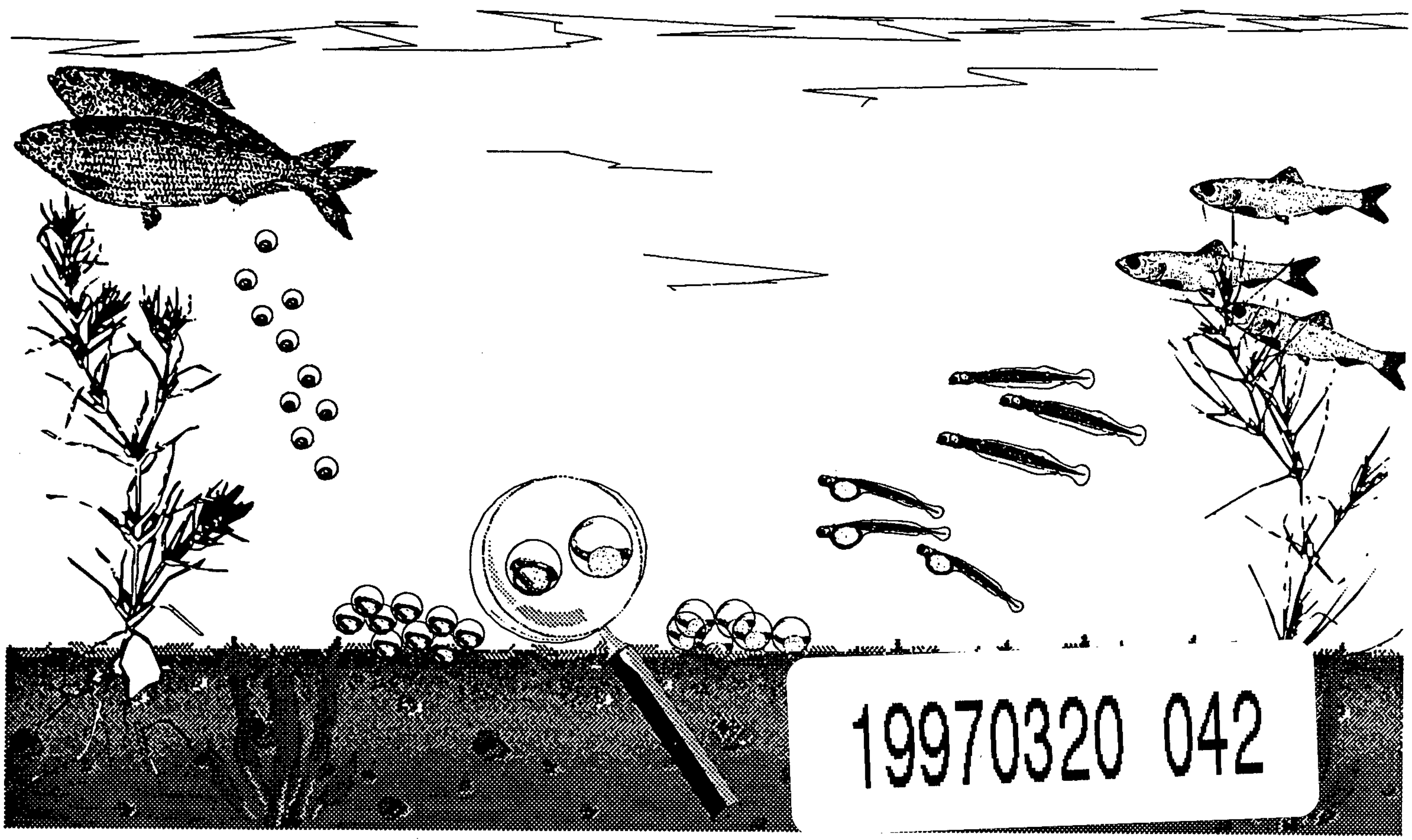
Evaluation of Habitat Suitability Index Models for Riverine Life Stages of American Shad, with Proposed Models for Premigratory Juveniles



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Evaluation of Habitat Suitability Index Models for Riverine Life Stages of American Shad, with Proposed Models for Premigratory Juveniles

By

Robert M. Ross, Thomas W. H. Backman, and Randy M. Bennett

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Washington, D.C. 20240

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Abstract. Field evaluations of existing habitat suitability index (HSI) models for spawning adults, eggs, and larvae of American shad (*Alosa sapidissima*) were conducted in 1990–92; initial models for juveniles in nursery habitats were developed. Fish abundance in various habitats of the upper Delaware River was quantified by (1) observation of adult spawning activity, (2) collection of eggs and larvae with metered plankton and drift nets, and (3) enumeration of juveniles by underwater observation and seining techniques. Regression analysis, principal component analysis, and range analysis were used to relate abundance to an array of physical habitat variables potentially influencing fish distributions.

The mean surface water temperature model for spawning adults (maximum suitability of 14–20° C) was supported at its lower limit, but the data suggest an upper-limit extension to 24.5° C. The mean water velocity model (maximum suitability of 0.3–0.9 m / s) was not supported, particularly at its lower limit (0–0.3 m / s), where adults spawned with equal frequency. Maximum suitability at the upper limit did not extend beyond 0.7 m / s. Spawning activity was observed in all habitat types examined but was greatest in runs and lowest in pools and riffle pools.

The HSI model for eggs and larvae in relation to surface water temperature (maximum suitability of 15–25° C) was supported for eggs and prolarvae. Surface water temperature was not predictive of postlarval relative density, however, because no reduction in density occurred at the upper thermal limit (26–27° C). The temporal variables date and time of day influenced egg and larval densities. Prolarvae were also affected positively by sample depth (among five remaining physical habitat variables), while postlarval densities were influenced positively by water depth and temperature. Only postlarvae showed differential habitat use: riffle pools were selected over riffles, channels, pools, and slopes.

No HSI model was previously developed for juvenile American shad in riverine habitats. We found four physical habitat variables that were correlated with juvenile abundance: water temperature, dissolved oxygen (covariates), river depth, and turbidity. The influence of these variables was habitat-specific (six types). Preliminary HSI models were developed for three of these variables. There was no overall effect of habitat type on juvenile relative abundance, indicating that juveniles use a wide variety of habitat types to their advantage in many nursery areas. In contrast to earlier life stages and spawning adults, premigratory juveniles appear to be habitat generalists.

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Suitability ranges for some physical variables were narrower or broader than previously assumed; moreover, the influence of these variables was found to be habitat specific. Therefore, American shad HSI models may be applied, with caution, on a comparative basis among river systems. Knowledge of the range and proportion of habitat types in each river system considered would be helpful in applying the models.

Key words: *Alosa sapidissima*, American shad, habitat suitability models, larval fishes, reproduction, river ecology.

Habitat suitability index (HSI) models were developed in the 1970's and 1980's to facilitate impact assessment, project planning, habitat management, and the understanding of species-habitat relations (U.S. Fish and Wildlife Service 1980; Schamberger et al. 1982; Stier and Crance 1985). These models provide information on species-habitat correlations that may be strengthened with further study. Many HSI models were developed on the basis of known literature and the Delphi process (Crance 1987). The Delphi process relies on extensive experience with the concerned species by the individuals queried. Habitat field studies were not directly employed to generate a data base from which many HSI models were developed. Such models are known as category-one suitability index curves (Bovee 1986).

The HSI models for American shad (*Alosa sapidissima*) were developed for spawning adults, eggs, and larvae in riverine habitats, but models for juveniles were limited to estuarine life during winter and spring (Stier and Crance 1985). Habitat variables deemed important to American shad during riverine components of their life history were mean surface water temperature during spawning season or egg–larval development period (spawning adults, eggs, and larvae) and mean water velocity during spawning season (spawning adults). Other variables such as depth, substrate, and cover were thought not to appreciably influence habitat use by American shad.

The purpose of our study was to evaluate the existing HSI models for American shad in riverine habitats by generating suitability index (SI) curves for the Delaware River, one of the most productive American shad river systems of the eastern United States. We compared our curves with existing SI curves (Stier and Crance 1985) and evaluated the models with statistical tests of correlation to habitat variables. We also developed habitat utilization relations for juvenile (premigratory) American shad in nursery habitats, and we propose HSI models for this previously ignored life stage. The category-two suitability index curves (Bovee 1986) generated by this study are considered to have broader applicability than those of category one, but they are not habitat preference curves.

Methods

Study Area

Field work was conducted on the Delaware River between the Delaware Water Gap (river kilometer 341, near East Stroudsburg, Pennsylvania) and Callicoon, New York (river kilometer 488; Fig. 1). The lower reaches of this river segment fall within the boundaries of the Delaware Water Gap National Recreational Area, while upper reaches fall within the Upper Delaware Scenic and Recreational River, both administered by the National Park Service (NPS). Fisheries jurisdiction includes the NPS and states of Pennsylvania, New Jersey, and New York.

Spawning Adults

We quantified spawning of adult American shad by counting spawning splashes over 5-min intervals between darkfall and 0100 h (Eastern Daylight Saving Time) from 16 April to 20 June 1991 and 13 April to 9 July 1992. To verify that such splashes were made by spawning American shad, we used spotlights from an anchored boat at two routinely observed spawning sites. Over a 1-h period at one site and 0.5 h at another, spotlights were activated for each splash heard within about 5 m of the boat. The number and species of fish observed and their behavior were recorded. We assume that, though every splash may not represent actual spawning and every spawning may not be accompanied by a splash, the level of surface activity is strongly correlated with actual spawning. Eleven sites (Table 1) representing five habitat types (Table 2) were sampled 1 to 17 times each by stationing two listeners on shore or in an

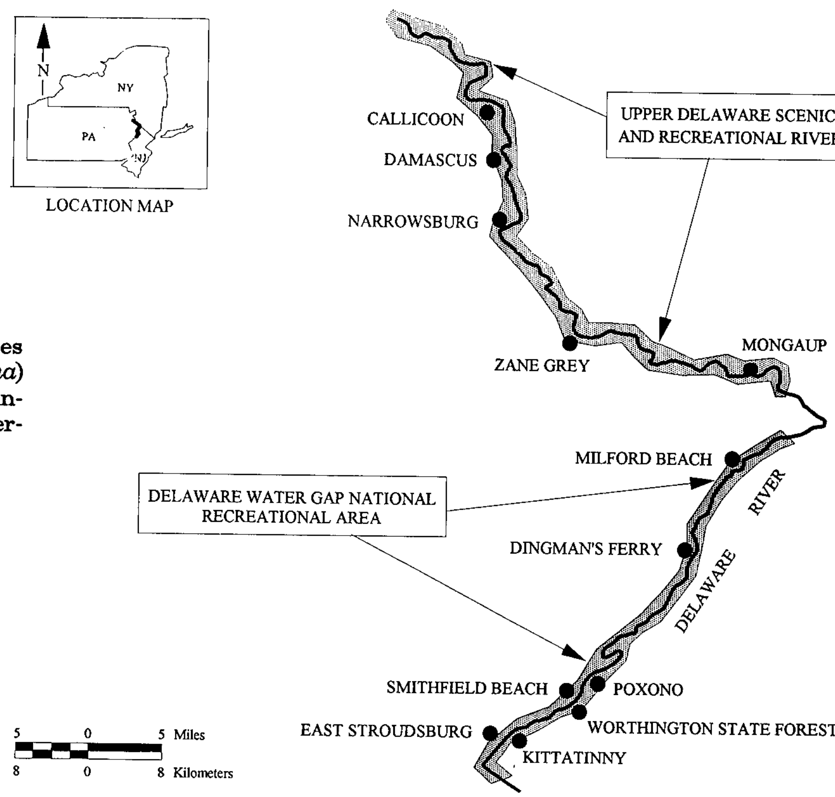


Fig. 1. Access sites for habitat studies of American shad (*Alosa sapidissima*) on the upper Delaware River, Pennsylvania, New York, and New Jersey.

anchored boat at each site. The average of the two counts of all splashes heard from a single location was recorded. After each count the following habitat variables were recorded: river depth (10 m from shore or at boat anchorage), middepth current velocity 10 m from shore or at anchorage (Marsh McBirney Model 201D), surface water temperature, dissolved oxygen (DO; YSI Model 51B), and turbidity. Turbidity was obtained from a turbidity meter reading (Markson nephelometer) of a refrigerated 25-mL surface water sample within 24 h. Habitat type was also determined and recorded at each count location.

We used principal component analysis (PCA; SAS 1987) to explore relations between spawning, five physical habitat variables, and five habitat

Table 1. *Access points and life stages sampled for American shad* (Alosa sapidissima) *on the upper Delaware River, 1990–92.*

		Life stage sampled			
Site access	River kilometer	Spawning adults	Eggs	Larvae	Juveniles
Kittatinny (New Jersey)	341	X			
Worthington State Forest (New Jersey)	346	X			
Smithfield Beach (Pennsylvania)	351	X	X	X	X
Poxono (New Jersey)	354	X			
Dingman's Ferry (Pennsylvania)	383	X	X	X	X
Milford Beach (Pennsylvania)	397	X	X	X	X
Mongaup (New York)	418	X			
Zane Grey (Pennsylvania)	447	X	X	X	X
Narrowsburg (Pennsylvania)	467	X			
Damascus (Pennsylvania)	479	X			
Callicoon (Pennsylvania)	488	X			

types. Observations were grouped into three classes by number of splashes: 0, 1–25, and >25. The average value for principal components (PC) 1 and 2 of each group was plotted on the PC1–PC2 grid, along with vectors for each habitat variable. Some degree of correlation among independent variables is assumed in PCA, but not in regression analysis (Lindeman et al. 1980). To further examine relations with specific habitat variables, we used linear and quadratic regressions (SAS 1987) with mean number of spawning splashes as the dependent variable and the above physical factors as independent variables. A null-hypothesis rejection level of $P \leq 0.05$ was set for these and all subsequent statistical tests. We used the Duncan multiple range test (SAS 1987) to rank and determine significant differences in spawning activity among five habitat types.

Eggs and Larvae

We sampled American shad eggs and larvae at four locations (Table 1), representing six habitat types (Table 2), with calibrated plankton nets in 1990 (8 May to 8 July), 1991 (16 April to 20 June), and 1992 (13 April to 9 July), from 1000 to 0230 h. Four types of plankton nets (all 500-µm mesh size) were used: (1) 61 × 25-cm (diameter) drift nets, (2) 35 × 35 × 61-cm benthic sled (inverted "U" opening) with 1-L bucket, (3) 2.5 × 0.5-m (diameter) bongo

Table 2. *Description and distribution of nine habitat types among the four primary access sites for American shad eggs, larvae, and juveniles on the upper Delaware River. Five of these habitats (channel, shallows with submerged aquatic vegetation [SAV], run, riffle pool, and pool) were also assessed for spawning adults.*

Habitat type	Sites where sampled[a]: Eggs and larvae	Sites where sampled[a]: Juveniles	Description of habitat
Channel	S,D,M	D	Deeper (2–5 m) portion of river where greatest current velocities found; typically the middle third of river width; little if any macrophytic vegetation anchored in substrate
Eddy		D	Zone of reversed current direction lateral to channel; includes shore areas with SAV but narrow shallow zone (rapid drop to >2 m)
Slope	S		Segment of river width shoreward of channel, 1–3.5 m deep, but not including shallow inshore zone; some attached macrophytes may be present, but not at high densities typically found inshore
SAV shallows	S,D,M	S,D,M,Z	Inshore zones, 0–1.5 m deep, where high densities of anchored macrophytic vegetation and low current velocities typically occur; sampled quantitatively only for juveniles
Run			Midriver stretch (spawning adults only) of relatively shallow (0.5–1.5 m) water of moderate to high current velocity (0.3–0.7 m / s)
Riffle	S,M,Z	S,M,Z	Zone of shallow (≤0.5 m) swift (typically >0.5 m / s) water with surface turbulence and aeration; SAV, if present, typically short (<0.25 m)
Riffle pool	Z	S,M,Z	Zone immediately downstream of a riffle, where water deepens suddenly and currents become variable in velocity and direction
Pool	Z		Relatively large river segment, where river width bulges and current velocities drop (<0.25 m / s); typically just upstream of a series of riffles
Tributary		W,M	Mouth and delta of a tributary stream, characterized by relatively cold water temperatures, steep water temperature gradients, and visibly dense suspended material ("drift")

[a] S = Smithfield Beach, D = Dingman's Ferry, M = Milford Beach, W = Delaware Water Gap, and Z = Zane Grey.

net with 1-L buckets, and (4) 6.1 × 2.4-m plankton seine with 2.4 × 1.2 × 2.4-m bag and 1-L bucket. Immediately before or after (or during in the case of drift-net and plankton-seine sets), the following physical variables were measured and recorded: average river depth, sample depth (from river depth and gear used), water temperature, DO, current velocity, and turbidity.

Drift nets were deployed in triplicate in riffle zones only and were secured with horizontal reinforcing bars attached to heavy metal stakes. Velocities through nets (used to calculate volumes of water sampled) were measured with a Marsh McBirney Model 201D current meter at the beginning and end of each 1.1–3.7-h set and averaged. The benthic sled was equipped with a propeller-style digital flow meter calibrated with the above-described current meter. It was deployed from a boat with a 1:1 winch mounted to a chest-high davit and 15 m of 3-mm steel rope. The sled was towed at a speed that allowed it to skid lightly on the river bottom. The bongo plankton seine was outfitted similarly but towed at a constant speed just below the surface.

The large plankton seine was also outfitted with a calibrated flow meter and held open by attachment to a horizontal 3.7-m steel rod. The preferred method of deployment was about 8 m behind the stern of the boat, which had to be anchored firmly to a large rock or similar object. Firm anchorage could not be found at one site, however, so dual grapnels were deployed off the bow to reduce boat drift and to increase flow through the net while dragging.

Volumes of water sampled per set by these techniques ranged as follows: drift net 20–964 m^3, benthic sled 1–93 m^3, bongo net 51–316 m^3, and plankton seine 11–4,806 m^3. All samples were carefully removed from nets or buckets and fixed in 10% formalin for transport to the laboratory, where they were transferred to 70% ethanol for preservation. All nonadhesive eggs 2.3–3.8 mm total diameter (after immersion >10 min in deionized water) with nuclear diameter ≤66% of total diameter were identified as American shad eggs. These criteria were necessary to distinguish American shad eggs from those of the white sucker (*Catostomus commersoni*), which spawns at the same time but produces fertile eggs with a different frequency distribution of egg to nucleus size (R. M. Ross and Bennett 1993). American shad yolk-sac (prolarvae) and post–yolk-sac (postlarvae) larvae were distinguished from anatomically similar larvae and identified by number of preanal myomeres, number of postanal myomeres, relative preanal length, and pigmentation patterns (Lippson and Moran 1974; Fuiman 1979; Holland-Bartels et al. 1990). We captured only larvae <20 mm in total length.

Egg and larval densities were calculated by dividing the number of eggs or larvae caught by the volume of water sampled by the net. Because four different sampling techniques were used to obtain all three life stages, the possibility of different catchability of the more mobile postlarval stage was considered. We assume no such difference for eggs and the weak-swimming prolarvae. We calculated sampling effort by gear type and habitat type (Table 3). Differential catchability of postlarvae was evaluated indirectly through comparison of observed postlarval densities in the same habitat for different gear types. Two comparisons met these requirements: (1) plankton seine and bongo net in near-surface channel habitat and (2) drift net with bongo net in riffle habitat. Postlarval densities in various habitats were also compared by gear type to determine whether different conclusions might be reached depending on sampling gear employed.

Relations between egg and larval density, physical habitat variables, and habitat type were explored with PCA by superimposing habitat type and life stage on the PC1–2 universe generated by physical habitat variables (available habitat). Life-stage density values were weighted by presence or absence (1 or 0) criteria to achieve better separation of life stages. Density values were also used as dependent variables in linear and quadratic regression analyses (SAS 1987) with the following continuous habitat variables: sample depth, river depth where sample was taken, water temperature, DO, current velocity, and turbidity. Also, the effect of habitat type on egg and larval abundance was tested by subjecting egg and larval densities to analysis of variance (ANOVA; SAS 1987) with four habitat types as class variables (Table 2; heavily vegetated shallows excluded because metered nets were not employed there, riffle pool excluded because of small sample size). We used the Duncan multiple range test (SAS 1987) to rank mean densities for each habitat type. Scatter plots were generated to illustrate egg and larval densities (nonzero values only) as a function of each measured physical habitat or temporal variable.

Inshore habitat zones with high densities of anchored macrophytic vegetation (submerged aquatic

vegetation, or SAV, excluding algal mats) were not sampled by metered plankton nets. Rather, this habitat type was sampled in 1990 with the 6.1- × 2.4-m plankton seine (unmetered) by walking the net from shore to a maximum depth of 1.5 m and hauling it in to shore for egg and larval collection. Water volumes sampled varied considerably with each haul, but 20 hauls were made in shallow SAV habitats at three different sites between 22 May and 8 July 1990.

Juveniles

Young-of-year juvenile American shad were quantified in six habitat types at five access sites with two different methods: seine hauls and quantitative underwater observations (Table 2). For seine-haul determinations, a 30.5- × 2.4-m (8-mm mesh) blackened beach seine, which captured only juveniles >35 mm total length, was deployed from the stern of a boat or, in shallow habitats, by walking the seine. Initial sets approximated a 10-m square before hauling toward a single landing site (on shore or in shallow riffles if required); however, in habitats subject to strong currents (channels, eddies, and riffle–eddy zones), square sets quickly became linear as the seine was hauled in.

Gear efficiency was estimated in SAV shallow habitats by deploying the seine by foot, as described above. A duplicate seine was then deployed just outside the first as a block net and the inner seine hauled to shore. The inner net was reset and pulled in two more times before the outer net was hauled to shore. Catchability was calculated as the number of juveniles in the first haul divided by the total number of fish captured. Catchability studies were conducted four times in SAV shallow habitats, but they were not feasible in other habitat types because of current-velocity and river-depth limitations.

Estimates of juvenile relative abundance were also obtained by dive counts on established 5-m-square grids in each habitat type at all access sites (Table 3). The corners of all grids were marked by 0.3-m spikes driven into the substrate and flagged with yellow plastic tape. Before any seining activity in a study area, counts of juveniles were made by a diver with mask, fins, snorkel, and slate. Counts were made by swimming up to the perimeter of a grid and then over the grid as needed. Three consecutive counts were used to determine a mean count for the grid. The above procedure was repeated after 10 min to assess the statistical variability of this count method.

The following habitat variables were obtained from the sample area either immediately before or after (allowing visibly disturbed water, if any, to pass first) both seine hauls and dive-count observations: average river depth, water temperature, DO, average current velocity, turbidity, and percent SAV cover. Percent SAV cover was estimated visually to the nearest 5% in each dive-count grid or seine-haul area.

Seine-haul and dive-count data were compared statistically, both overall and within each habitat type, with Pearson correlation coefficients (SAS 1987). We used PCA to relate juvenile relative abundance to habitat by superimposing habitat type and dive or seine juvenile counts on the universe of vectors representing available physical habitat. The relation between juvenile abundance (dependent variable) and each measured habitat variable was then examined by regression analysis (SAS 1987), both overall and by habitat type. Both of these analyses were performed independently with dive-count data and combined dive-and-seine data sets. The effect of habitat type on juvenile relative abundance was determined by ANOVA with six habitat types as class variables.

Table 3. *Sampling effort in the upper Delaware River for American shad eggs and larvae by gear type for each habitat type. Numbers represent volumes of river water sampled in cubic meters, with percentage of total volume for each habitat type (gear type under "all habitats") in parentheses.*

Gear type	Pool		Channel		Riffle[a]		Slope		All habitats	
Bongo net	3,029	(90)	10,651	(45)	3,972	(7)	290	(72)	17,942	(21)
Plankton seine			12,115	(51)	28,535	(49)			40,650	(47)
Drift net					25,709	(44)			25,709	(30)
Benthic sled	347	(10)	890	(4)	50	(0.1)	111	(28)	1,398	(2)

[a] Includes riffle pool habitat.

Results

Spawning Adults

Over a 1-h observation period at one site and 0.5 h at another, 24 and 8 splashes were heard and spotlighted within 5 m of the boat. Each splash was caused by adult American shad in a tight group of 2–6 individuals. Observed behavior included dashing or darting (often parallel to one or more other fish), tight circling with another fish near the surface, and rolling near the surface parallel to another fish. Gamete release was not observed.

Spawning activity was greatest between 30 April and 17 June and between 2100 and 0100 h (Figs. 2 and 3). In PCA, component vectors associated with the greatest number of spawning splashes (Fig. 4) were water temperature (positive relation [+]), DO (negative [−]), and current velocity (−). Regression analysis showed significant relations with water temperature (+) and DO (−), corroborating PCA results except for current velocity (Table 4; Figs. 5–8). The run habitat ranked significantly higher in spawning activity than other habitat types; pool and riffle pool were lowest (Table 5).

Eggs and Larvae

Postlarval density analyses showed no evidence of differential catchability by gear type. Though the mean density in channels was 2–3 times higher with bongo than plankton seine (Table 6), plankton-seine data came from a single location versus three sites for the bongo. In addition, habitat density ranks were the same regardless of gear used to sample these habitats (Fig 5.). Even more conclusive was the ratio of drift-net to bongo-net densities for prolarvae and postlarvae (Table 7). Postlarvae were an order of magnitude denser in drift nets than bongo nets set in riffle zones, a result opposite of expectations were net avoidance by postlarvae possible (drift nets have much smaller openings than bongo nets). The greater numbers of postlarvae likely result from their occupying a higher position in the water column (eggs and prolarvae drift nearer to the substratum). Possibility of greater postlarval escape from the benthic sled is also likely owing to the slow tow velocities needed to keep the sled on the bottom. However, sled volumes accounted for only 2% of the total river volume sampled (Table 3).

American shad eggs were found in greatest densities from 8 May to 18 June over the 3-year sampling period, prolarvae 8 to 17 June, and postlarvae 14 May to 9 July (Fig. 9). Over the diel cycle, eggs became numerous between 2000 and 2400 h, prolarvae between 1800 and 0030 h, and postlarvae over all hours sampled (0930–0230 h; Fig. 10). In PCA, American shad eggs showed association with higher current velocities and shallower river depths than larvae (Fig. 11). Riffle habitat was more closely and slope habitat less closely aligned

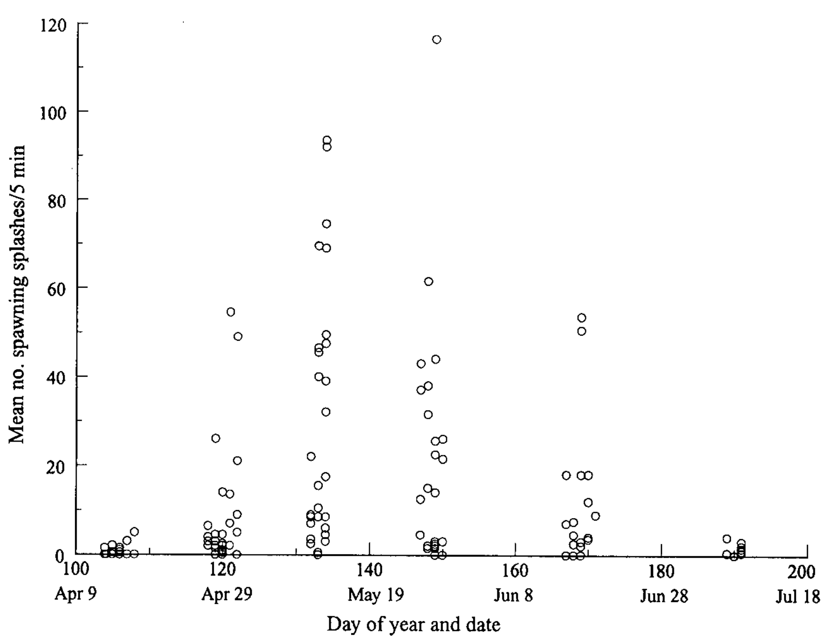


Fig. 2. Relation between mean number of spawning splashes per 5 min and date for adult American shad in the upper Delaware River.

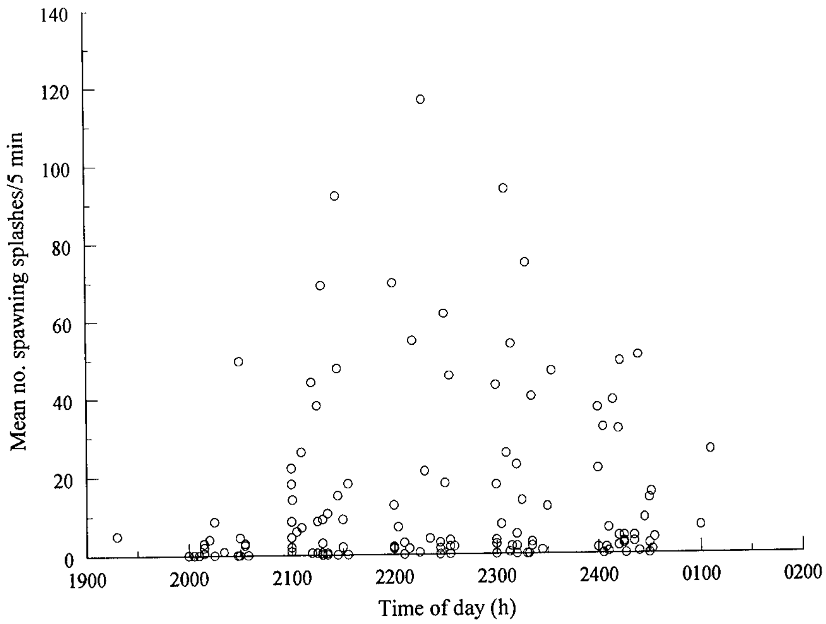


Fig. 3. Relation between mean number of spawning splashes per 5 min and time of day (Eastern Daylight Saving Time [DST]) for adult American shad in the upper Delaware River.

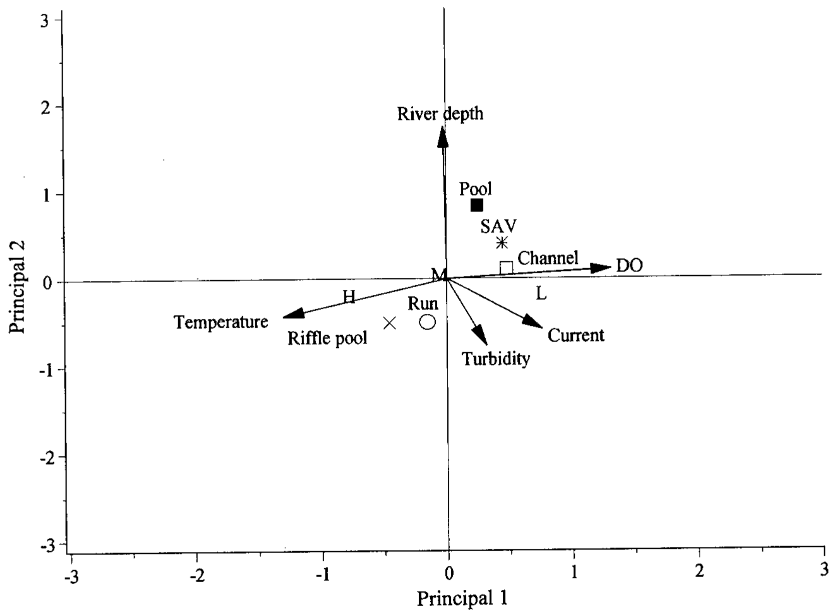


Fig. 4. Principal component analysis of the number of adult spawning splashes (low, moderate, or high) in relation to four physical habitat variables in the upper Delaware River. Mean values for low, moderate, and high numbers of spawning splashes are plotted as *L*, *M*, and *H*. Vectors are drawn to twice their calculated length (eigenvector output) for visual enhancement.

Table 4. *Linear and quadratic regression analyses among five physical habitat variables and number of splashes by spawning adult American shad heard on the upper Delaware River.*

Habitat variable	Regression type	Degrees of freedom	*F* value	*P*	R^2
Water temperature	Linear	1, 128	10.8	0.001**	0.08
	Quadratic	2, 127	9.0	0.011*	0.12
Dissolved oxygen	Linear	1, 113	7.6	0.007**	0.06
	Quadratic	2, 112	5.1	0.12	0.08
Current velocity	Linear	1, 128	0.0	0.90	0.00
	Quadratic	2, 127	0.95	0.17	0.01
Depth	Linear	1, 128	0.12	0.74	0.00
	Quadratic	2, 127	0.25	0.54	0.00
Turbidity	Linear	1, 106	3.70	0.06	0.03
	Quadratic	2, 105	2.13	0.12	0.04

*, ** Significant at 0.05 and 0.01 levels.

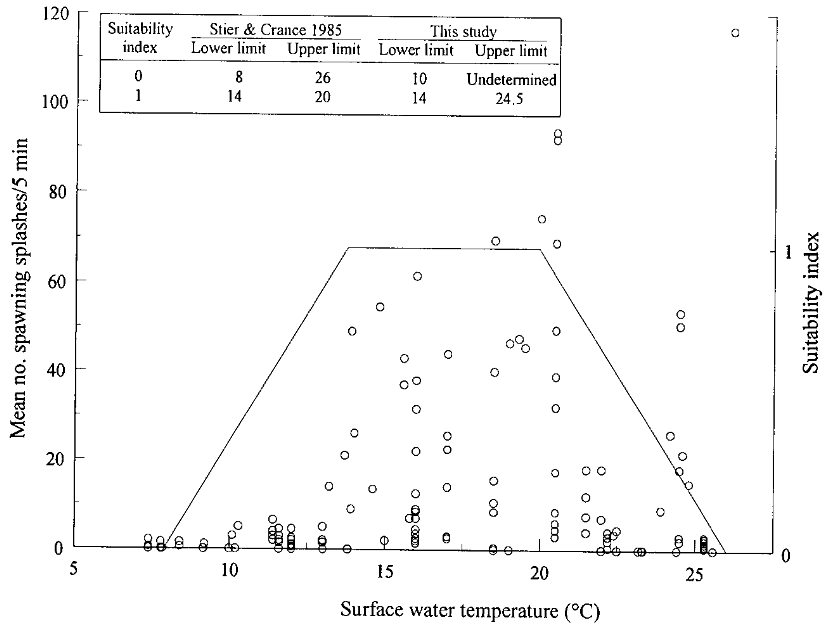


Fig. 5. Habitat suitability index (HSI) model for spawning adult American shad (Stier and Crance 1985) superimposed on relation between mean number of spawning splashes per 5-min interval and surface water temperature for adult American shad in the upper Delaware River. A comparison of lower parameter limits for minimum (0) and maximum (1) suitability between plotted data and the Stier and Crance (1985) model is presented (*inset*).

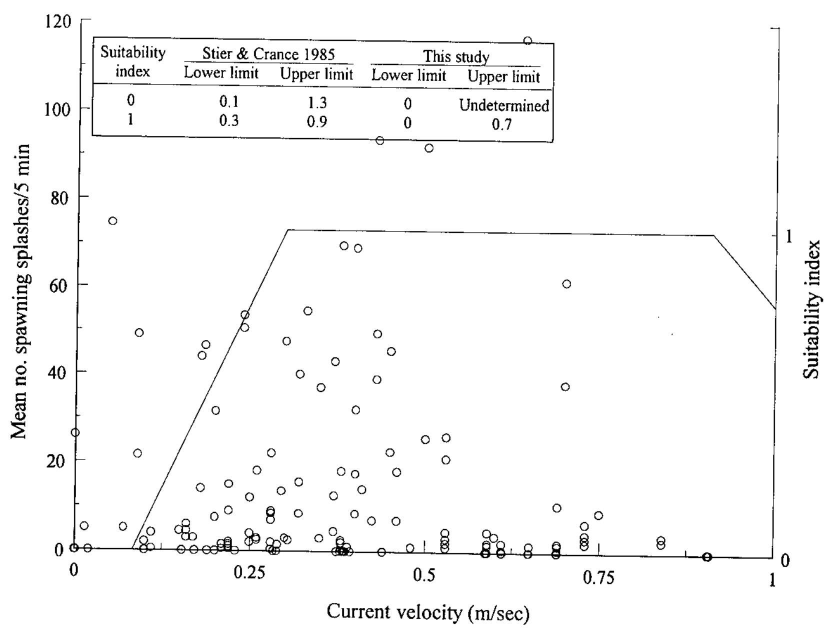


Fig. 6. HSI model for spawning adult American shad (Stier and Crance 1985) superimposed on the relation between mean number of spawning splashes per 5-min interval and current velocity for adult American shad observed in the upper Delaware River. A comparison of lower parameter limits for minimum (0) and maximum (1) suitability between plotted data and the Stier and Crance (1985) model is presented (*inset*).

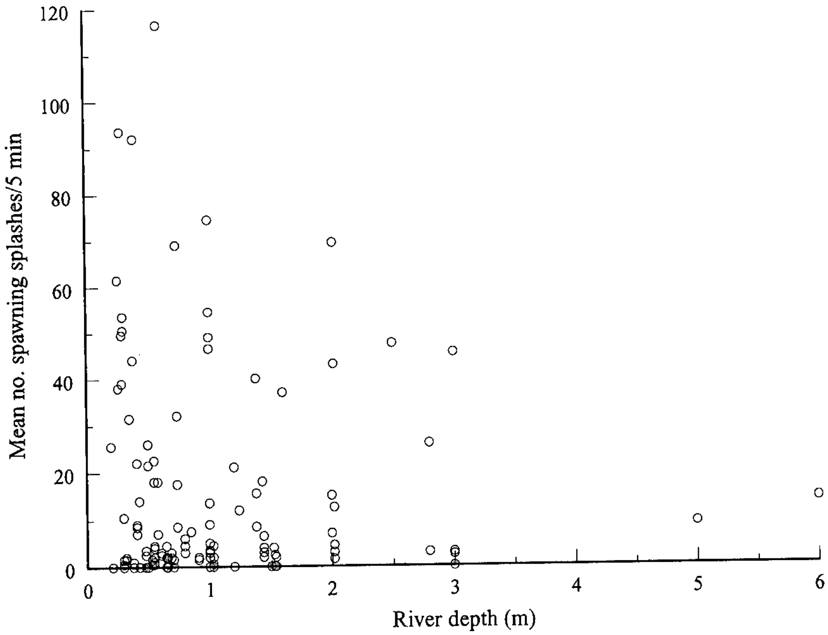


Fig. 7. Relation between mean number of spawning splashes per 5-min interval and river depth for adult American shad in the upper Delaware River.

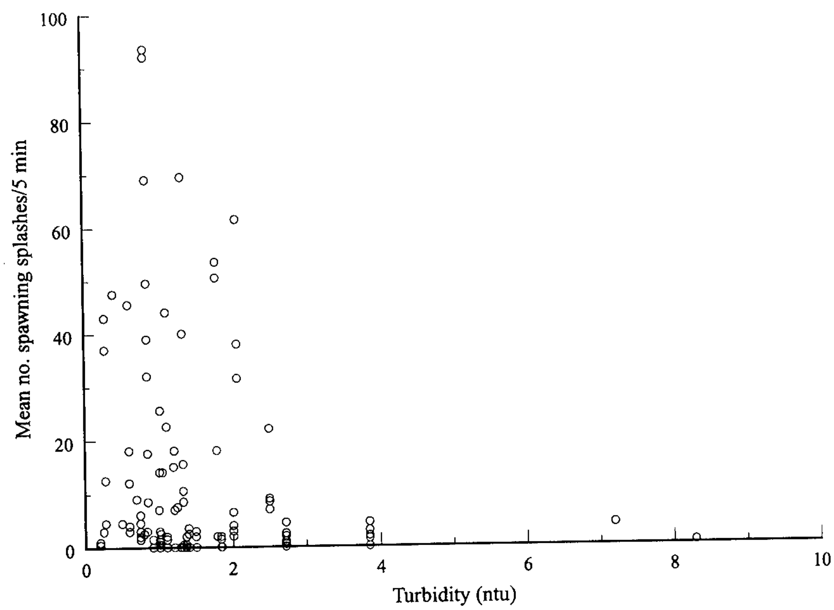


Fig. 8. Relation between mean number of spawning splashes per 5-min interval and turbidity for adult American shad in the upper Delaware River.

Table 5. *Duncan's multiple range test for the effect of habitat type on spawning activity by American shad in the upper Delaware River. Error degrees of freedom = 137,* F *= 5.75,* P *< 0.001.*

Habitat type	*n*	Mean no. spawning splashes	Duncan group
Run	33	23.1	A
Channel	34	10.5	B
SAV shallows	43	10.2	B
Riffle pool	14	5.1	B
Pool	18	1.6	B

with egg distribution than with larval distribution. Prolarvae were associated with river depth (+) and current velocity (-) to a greater degree than postlarvae or eggs. Channel and pool habitats represented prolarval distribution better than postlarvae or eggs. Postlarvae were associated with higher water temperatures and lower turbidities than either prolarvae or eggs. Little difference in habitat use was observed.

Regression analyses corroborated some PCA-identified relations but indicated the inverse or no relation for others (Table 8; Figs. 12–16). Egg density, for example, showed no relation to current velocity or river depth, but a positive relation to sample depth. Prolarval density increased only with sample depth and showed no relation to current velocity. Postlarvae showed positive relations with sample depth and ambient water temperature among the six variables examined.

Other notable findings concern the range over which eggs or larvae were found for each habitat variable (Table 9). Prolarvae, for example, were found over a much shorter portion of the sampling season than eggs or postlarvae. Eggs were found even 3 weeks later than prolarvae. Eggs and prolarvae escaped capture during most of the lighted

Table 6. *ANOVA and Duncan multiple range tests for effect of habitat type in the upper Delaware River on American shad density at three life stages. Postlarval densities are also partitioned by gear type to assess potential differences in gear catchability for this life stage.*

Life stage or gear	DF		*F*	*P*	Duncan multiple range test			
	Model	Error			Mean	*n*	Habitat	Group
Egg	4	216	0.8	0.53	0.396	11	Slope	A
					0.213	81	Riffle	A
					0.103	103	Channel	A
					0.056	16	Pool	A
					0.009	10	Riffle pool	A
Prolarva	4	216	1.1	0.37	0.0013	103	Channel	A
					0.0008	16	Pool	A
					0.0006	10	Riffle pool	A
					0.0004	81	Riffle	A
					0.0000	11	Slope	A
Postlarva	4	216	3.4	0.01	0.011	10	Riffle pool	A
					0.002	81	Riffle	B
					0.002	103	Channel	B
					0.001	16	Pool	B
					0.000	11	Slope	B
Bongo net	2	73	0.5	0.59	0.0016	62	Channel	A
					0.0007	10	Pool	A
					0.0000	4	Slope	A
Plankton seine	1	26	3.72	0.06	0.0106	10	Riffle pool	A
					0.0006	18	Channel	A
Drift net	0	80			0.0021	81	Riffle	—
Benthic sled	2	33	0.51	0.61	0.004	23	Channel	A
					0.002	6	Pool	A
					0.000	7	Slope	A

Table 7. *Comparison of egg, prolarval, and postlarval densities obtained by drift or bongo net in riffle habitats in the upper Delaware River.*

Gear	Date	Eggs	Prolarvae	Postlarvae
Drift net	15 Jun 92	0.175	0.005	0.009
		0.082	0.000	0.000
		0.160	0.004	0.004
	16 Jun 92	0.036	0.000	0.000
		0.010	0.000	0.010
		0.032	0.000	0.005
	17 June 92	0.434	0.000	0.030
		0.876	0.000	0.038
	Mean	0.226	0.001	0.012
Bongo net	15 Jun 92	0.349	0.001	0.000
		0.695	0.000	0.002
	16 Jun 92	0.016	0.000	0.001
		0.054	0.006	0.006
	17 June 92	1.306	0.004	0.006
	Mean	0.484	0.002	0.003
Ratio drift to bongo		0.47	0.50	4.0

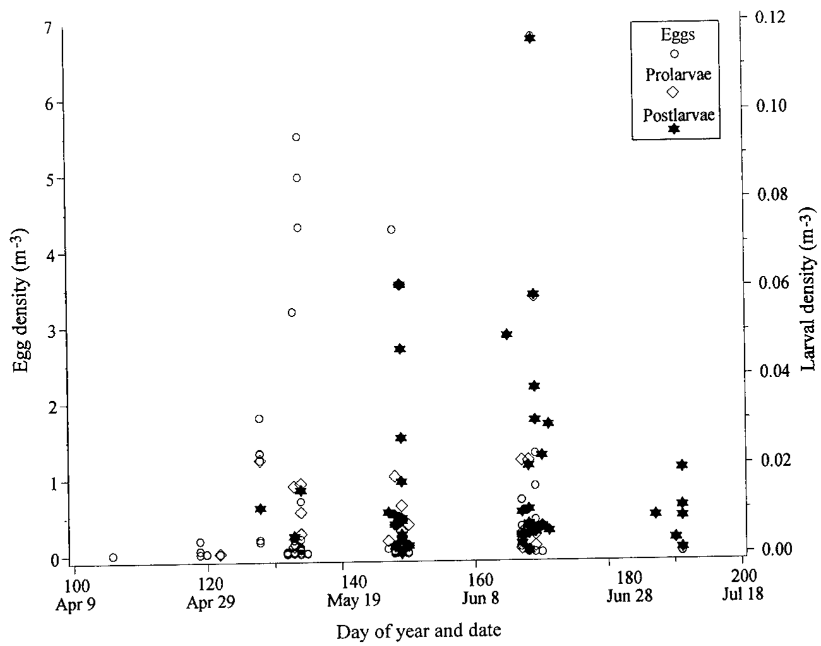


Fig. 9. Relations between American shad egg and larval density and date on the upper Delaware River.

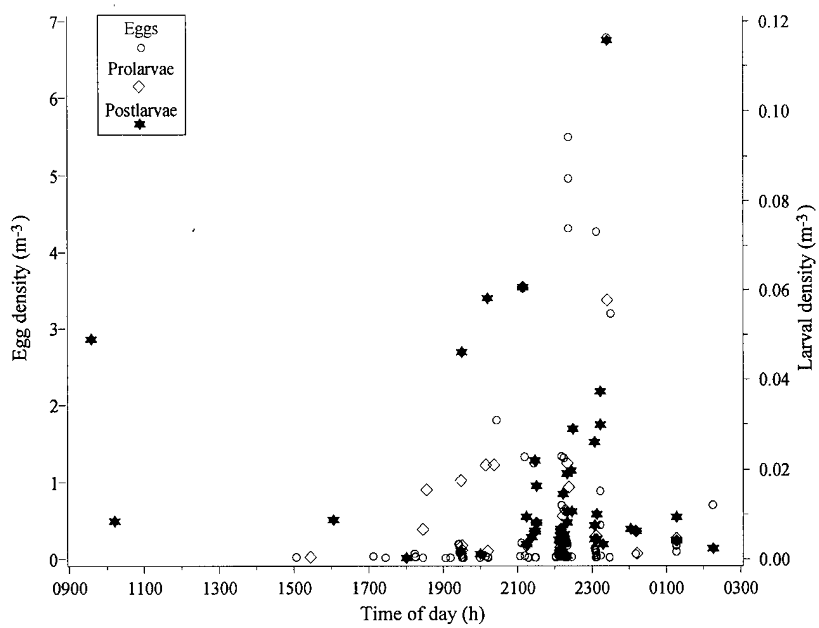


Fig. 10. Relations between American shad egg and larval density and time of day (DST) on the upper Delaware River.

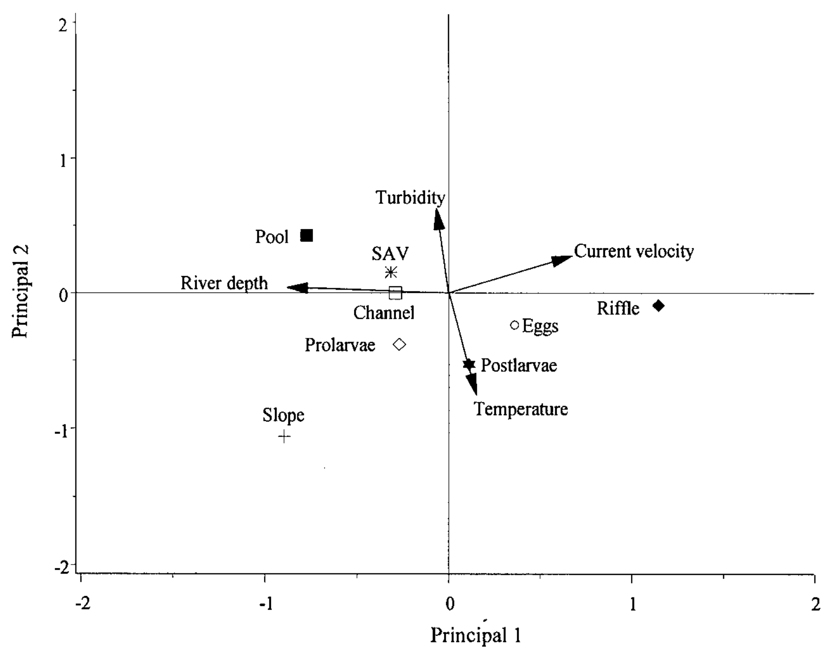


Fig. 11. Principal component analysis for the densities of American shad eggs, prolarvae, and postlarvae as they relate to six physical habitat variables and four habitat types in the upper Delaware River. Vectors are drawn to twice their calculated length (eigenvector output) for visual enhancement.

Table 8. *Linear regression of American shad egg and larval densities on six physical habitat variables in the upper Delaware River. DF refers to error degrees of freedom.*

Habitat variables	Life stage Eggs	Prolarvae	Postlarvae
Sample depth			
DF	227	227	227
R^2	0.03	0.03	0.05
Slope	+	+	+
P	0.007**	0.009**	0.0006***
River depth			
DF	228	228	228
R^2	0.01	0.01	0.00
Slope	–	+	+
P	0.19	0.26	0.45
Temperature			
DF	227	227	227
R^2	0.00	0.01	0.04
Slope	+	+	+
P	0.36	0.12	0.003**
Dissolved oxygen			
DF	226	226	226
R^2	0.00	0.00	0.01
Slope	+	–	–
P	0.81	0.21	0.16
Current velocity			
DF	222	222	222
R^2	0.01	0.01	0.02
Slope	–	–	–
P	0.13	0.13	0.06
Turbidity			
DF	191	191	191
R^2	0.00	0.00	0.00
Slope	–	–	–
P	0.82	0.77	0.79

**, ***Significant at 0.01 and 0.001 levels.

portion of the diel cycle. Most river depths were inhabited by both eggs and larvae. Larvae were not found until water temperatures reached 13° C, but eggs and larvae were found up to the highest temperatures sampled (26.6° C). Eggs and larvae were found at all but the highest (>1.1 m/s) current velocities. Egg distribution was limited to turbidities ≤2.7 ntu, while larvae were restricted to turbidities <2.1 ntu.

Analysis of variance for the effect of habitat type (five classes) on egg and larval density showed no effect on eggs or prolarvae but a significant effect on postlarvae, with the riffle pool habitat showing higher densities than all others (Table 6). The Duncan multiple range test further showed that eggs concentrated in slope > riffle > channel > pool > riffle pool; prolarvae in channel > pool > riffle pool > riffle > slope; and postlarvae in riffle pool >> riffle > channel > pool > slope.

Juveniles

Catchability of juvenile American shad in SAV habitats ranged from 52 to 80%; the average was 68% (Table 10). There was no correlation between seine-haul counts and dive counts overall, but correlations were found in two specific habitat types: SAV (strongly correlated) and riffle (Table 11).

Juveniles were found from 20 June to 3 October and at all hours sampled from 0353 to 2345 h (Figs. 17 and 18). Principal component analysis of the 1991 data alone showed the relative abundance of juveniles to be related positively to water temperature and river depth but negatively to turbidity; however, these relations were negated when 1992 data (with much cooler summer water temperatures) were included (Fig. 19). Closer relations (positive or negative) to riffle pool, eddy, and SAV habitats were observed than to riffle and channel habitats.

Regression analyses with dive counts alone or dive and seine-haul counts showed significant relations for two of six physical habitat variables (Table 12; Figs. 20–22). Relative abundance of juvenile American shad was directly related to water temperature and inversely to DO. A different pattern of significant relations emerged, however, when regressions were performed by habitat type (Table 13). Water temperature was an important determinant of relative abundance only in riffle habitat, while river depth became important in SAV habitat. Current velocity and turbidity emerged as determinants of relative abundance almost exclusively in tributaries (a linear relation was found for current velocity in riffle pool). Percent SAV cover was important in eddy (dive counts only) and SAV habitats.

Analysis of variance for the effect of habitat type on juvenile relative abundance showed no effect (Table 14). A t-test showed no difference between the first and second (10 min later) dive count on grids (regardless of habitat). Means ± standard errors were 33 ± 9 and 37 ± 11. Neither means (DF = 48, t = 1.54, P = 0.13) nor variances (DF = 48, F = 1.41, P = 0.24) were significantly different.

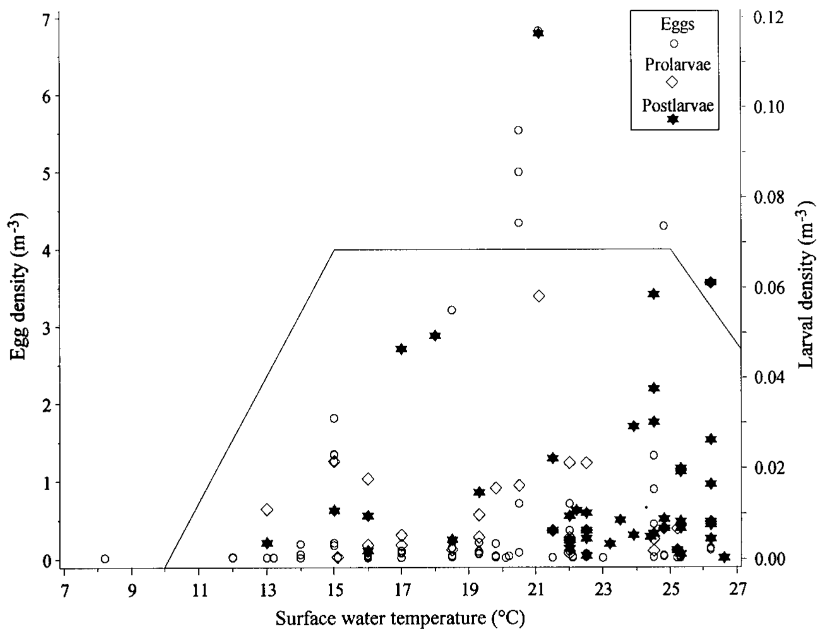


Fig. 12. HSI model for egg and larval American shad (Stier and Crance 1985) superimposed on the relations between egg and larval density and surface water temperature observed in the upper Delaware River. The base and peak of the HSI model represent suitability indices of 0 and 1, respectively.

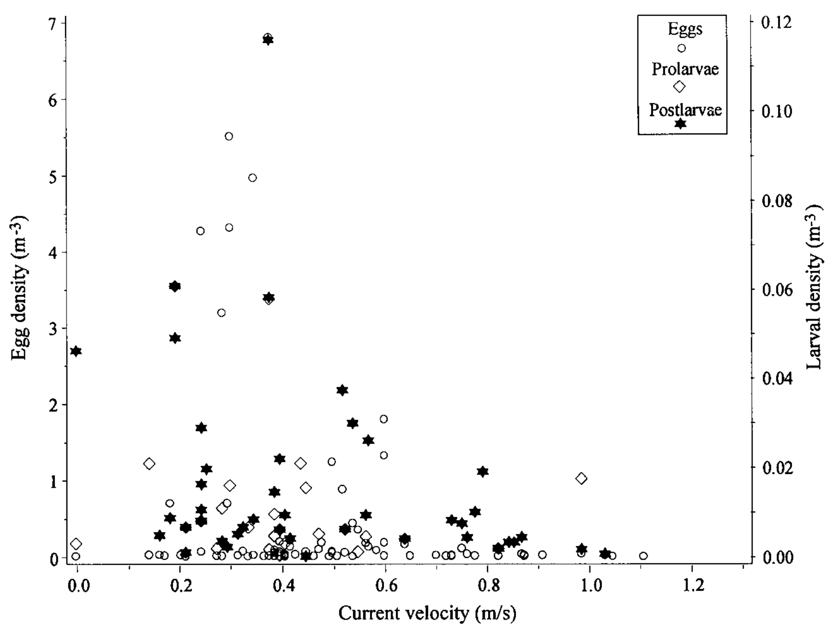


Fig. 13. Relations between American shad egg and larval density and current velocity in the upper Delaware River.

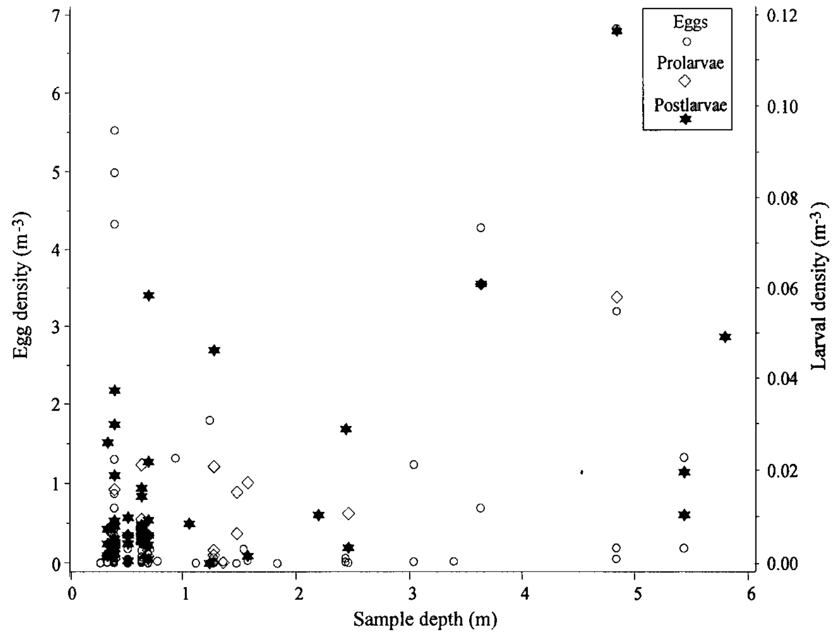


Fig. 14. Relations between American shad egg and larval density and sample depth in the upper Delaware River.

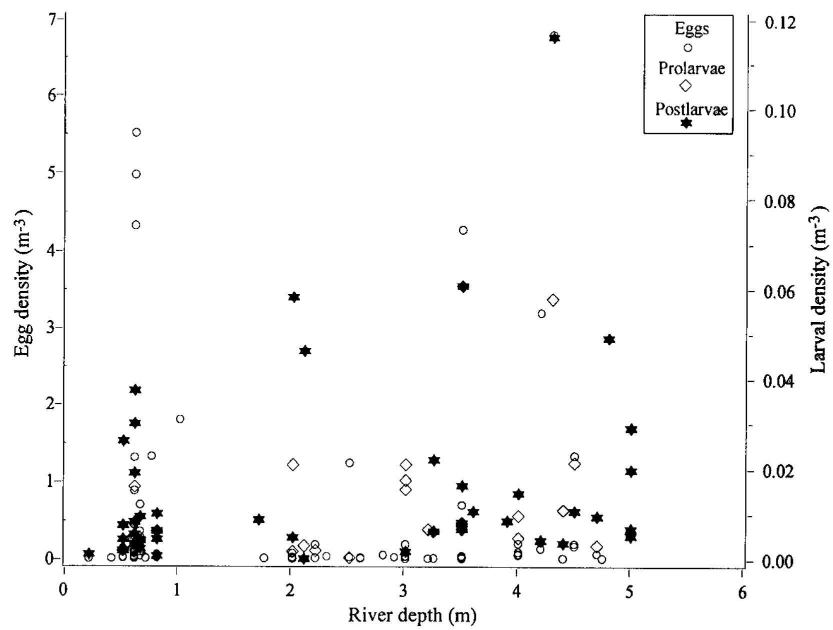


Fig. 15. Relations between American shad egg and larval density and river depth in the upper Delaware River.

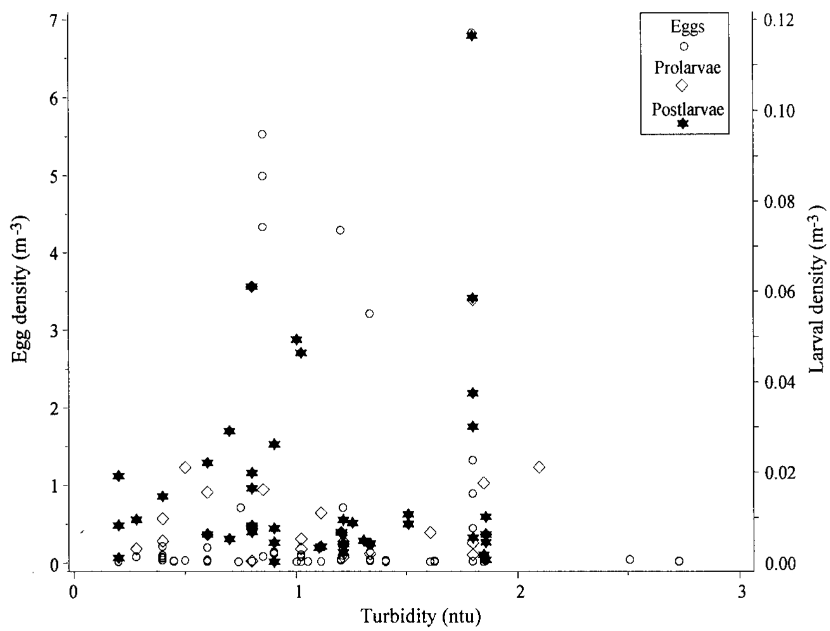


Fig. 16. Relations between American shad egg and larval density and turbidity in the upper Delaware River. Fewer than 10 samples were taken at higher turbidity readings (between 4.0 and 8.5 ntu); none contained eggs or larvae.

Table 9. *Comparison of the measured ranges of date, time of day, and six physical habitat variables over which American shad eggs and larvae were observed and sampled in the upper Delaware River.*

Variable and life stage	Median observation	Range		
		Observed	Sampled	%[a]
Date				
Eggs	14 May	16 Apr–09 Jul	13 Apr–09 Jul	97
Prolarvae	28 May	02 May–18 Jun	13 Apr–09 Jul	55
Postlarvae	16 Jun	08 May–09 Jul	13 Apr–09 Jul	72
Time of day (h)				
Eggs	2217	1506–2628	0954–2628	67
Prolarvae	2214	1543–2530	0954–2628	59
Postlarvae	2229	0954–2628	0954–2628	100
Sample depth (m)				
Eggs	0.50	0.20–4.5	0–5	86
Prolarvae	0.55	0.25–4.0	0–5	75
Postlarvae	0.50	0.25–4.8	0–5	91
River depth (m)				
Eggs	2.0	0.2–4.8	0–6	77
Prolarvae	2.0	0.2–4.8	0–6	77
Postlarvae	2.1	0.5–5.0	0–6	80
Temperature (° C)				
Eggs	19.6	8.2-26.6	7.4-26.6	96
Prolarvae	21.5	13.0-26.2	7.4-26.6	69
Postlarvae	23.5	13.0-26.6	7.4-26.6	69
Dissolved oxygen (mg / L)				
Eggs	9.5	7.6–11.8	7.6–14.1	65
Prolarvae	9.3	7.6–11.8	7.6–14.1	65
Postlarvae	9.1	7.6–11.8	7.6–14.1	65
Current velocity (m / s)				
Eggs	0.45	0.01–1.10	0.01–1.28	76
Prolarvae	0.39	0.01–0.98	0.01–1.28	76
Postlarvae	0.40	0.01–1.02	0.01–1.28	80
Turbidity (ntu)				
Eggs	1.2	0.20–2.72	0.20–8.30	31
Prolarvae	1.1	0.28–2.09	0.20–8.30	22
Postlarvae	1.1	0.20–1.85	0.20–8.30	20

[a] Units observed / units sampled × 100.

Table 10. *Catchability of juvenile American shad by seining in SAV habitats (shallows having submerged aquatic vegetation) in the upper Delaware River.*

		No. juveniles captured					
		Inner net haul[a] no.			Outer net		Catchability[b]
Date	Site	1	2	3	haul	Total	(%)
11 Jul 91	Zane Grey	14	3	0	10	27	52
20 Aug 91	Milford	8			2	10	80
09 Sep 91	Dingman's Ferry	7	1	2	2	12	58
11 Sep 91	Zane Grey	8	1	1	0	10	80
Total		37	5	3	14	59	68

[a] Inner seine net hauls were made within an encircling (outer) block net.
[b] Defined as the percentage of fish captured by the first inner net haul of the total fish captured by all net hauls.

Discussion

Spawning Adults

Determination of habitat requirements for spawning adult American shad was limited in this study to measurement of only five physical habitat variables. Habitat use could have been quantified in other ways, as by seine deployment and electrofishing techniques. Such methods are costly in terms of time and resources, however, and still would not ascertain the number of fish actually spawning in a specific location. Splashes, on the other hand, are documented indications of spawning activity (Marcy 1972; Chittenden 1976) and are readily obtained with a minimum expenditure of time and resources. All 32 spotlighted splashes were verified to be from adult American shad exhibiting courtship and spawning behavior. The technique was thus valid and useful in quantifying spawning activity in this species.

A major problem with either technique is scale and habitat resolution. American shad seemed to spawn over large areas, both longitudinally (>100 m) and laterally, often encompassing several habitat types. Physical habitat variables, especially depth and current velocity, vary longitudinally and (especially) laterally from a single location on shore. However, within the habitat limitations acknowledged, the results may be interpreted reliably.

Principal component analysis identified the following parameters as important correlates of spawning: water temperature (+) > DO (−) > current velocity (−). Regression analysis identified significant relations with water temperature and DO level. Under equilibrium saturation conditions DO is an inverse function of water temperature. Such oxygen-saturated conditions are likely to exist in the river during the spawning season (April–June) when primary productivity (and thus photosynthesis) has not yet peaked. Thus a water temperature relation can be inferred from the DO relation. Dissolved oxygen is not thought to affect American shad behavior or physiology if it remains above 5 mg / L (Chittenden 1969). Accordingly, we may ignore DO as an independent variable important to this life stage.

These results indicate that, other than temporal variables (date and time of day), water temperature is the primary environmental determinant of adult spawning activity among those variables measured. There is considerable evidence that ambient water temperature is a causative factor in the initiation of migration into natal rivers as well (Leggett and Whitney 1972). Though not demonstrated specifically in American shad, temperature also plays a role in stimulating ovarian maturation in fishes (e.g., Sundararaj and Vasal 1976). Our observed increase in

Table 11. *Pearson correlation coefficient tests, overall and by habitat type, for paired seine and dive counts of juvenile American shad in the upper Delaware River.*

Habitat type	*n*	*R*	*P*
All	39	0.05	0.78
Submerged aquatic vegetation	18	0.60	0.009**
Riffle	5	0.94	0.02*
Riffle pool	6	−0.40	0.43
Eddy	6	0.32	0.54
Channel	2	Insufficient data	
Tributary	2	Insufficient data	

*, **Significant at 0.05 and 0.01 levels.

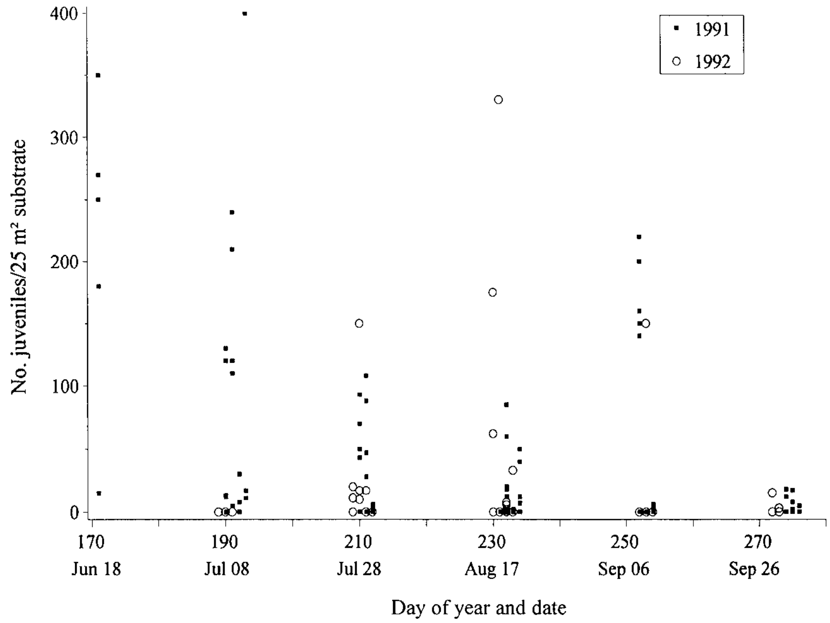


Fig. 17. Relation between juvenile American shad relative abundance and date on the upper Delaware River.

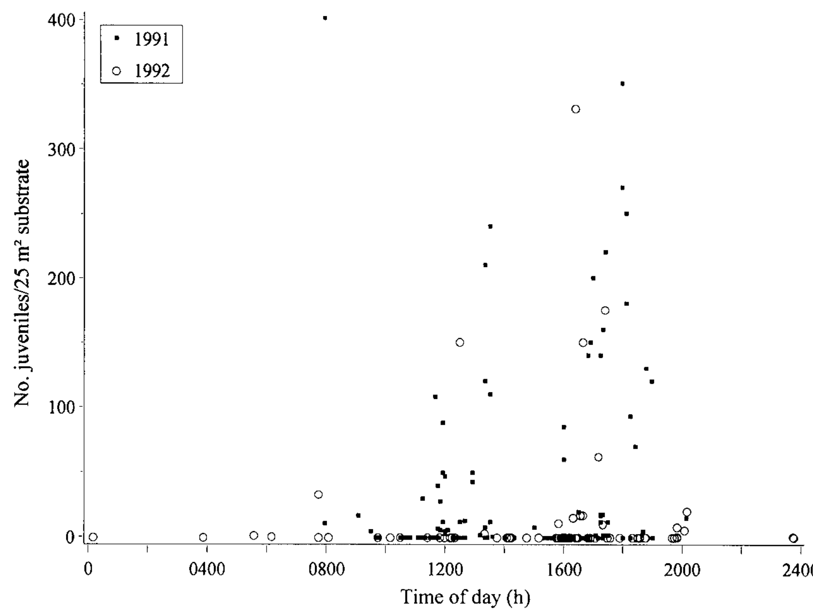


Fig. 18. Relation between juvenile American shad relative abundance and time of day (DST) on the upper Delaware River.

Fig. 19. Principal component analysis for American shad juvenile abundance in relation to five physical habitat variables and five habitat types in the upper Delaware River. Vectors are drawn to twice their calculated length (eigenvector output) for visual enhancement.

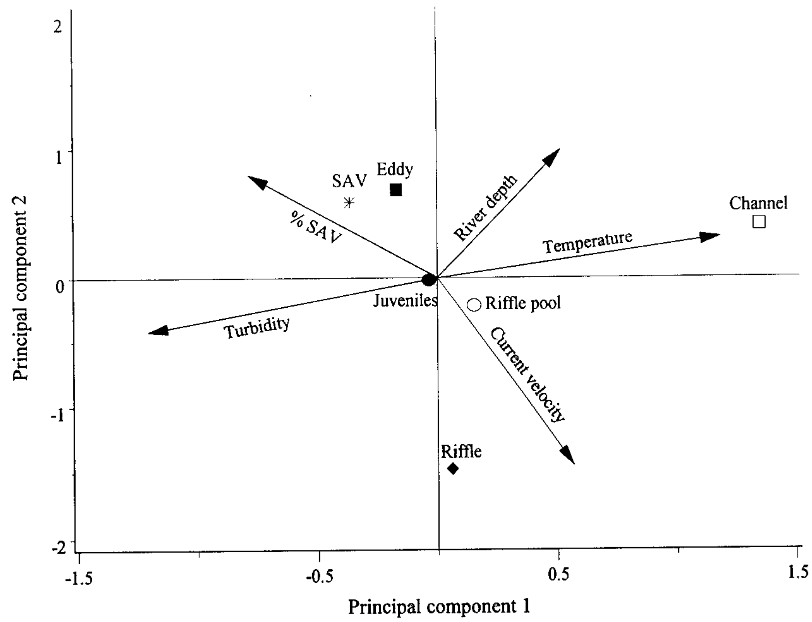


Table 12. *Linear and quadratic regression analyses of the effect of six physical habitat variables on abundance of juvenile American shad in the upper Delaware River measured by both dive and seine counts or by dive counts only. DF refers to error degrees of freedom.*

Physical variable	Both dive and seine: Linear	Both dive and seine: Quadratic	Dive only: Linear	Dive only: Quadratic
River depth				
DF	245	244	204	203
R^2	0.09	0.02	0.01	0.01
Slope	+	–	+	+
P	0.15	0.10	0.20	0.26
Temperature				
DF	248	247	206	205
R^2	0.03	0.03	0.04	0.05
Slope	+	+	+	+
P	0.01*	0.03*	0.002**	0.004**
Dissolved oxygen				
DF	248	247	206	205
R^2	0.01	0.02	0.02	0.02
Slope	–	–	–	–
P	0.12	0.13	0.04*	0.09
Current velocity				
DF	243	242	202	201
R^2	0.00	0.00	0.01	0.01
Slope	–	+	+	–
P	0.83	0.90	0.22	0.40
Turbidity				
DF	231	230	191	190
R^2	0.02	0.02	0.02	0.02
Slope	–	–	–	–
P	0.03*	0.07	0.07	0.11
Percent submerged aquatic vegetation				
DF	239	238	201	200
R^2	0.01	0.01	0.01	0.01
Slope	+	–	+	+
P	0.16	0.27	0.24	0.46

*, ** Significant at 0.05 and 0.01 levels.

Fig. 20. Relation between juvenile American shad relative abundance and water temperature in the upper Delaware River.

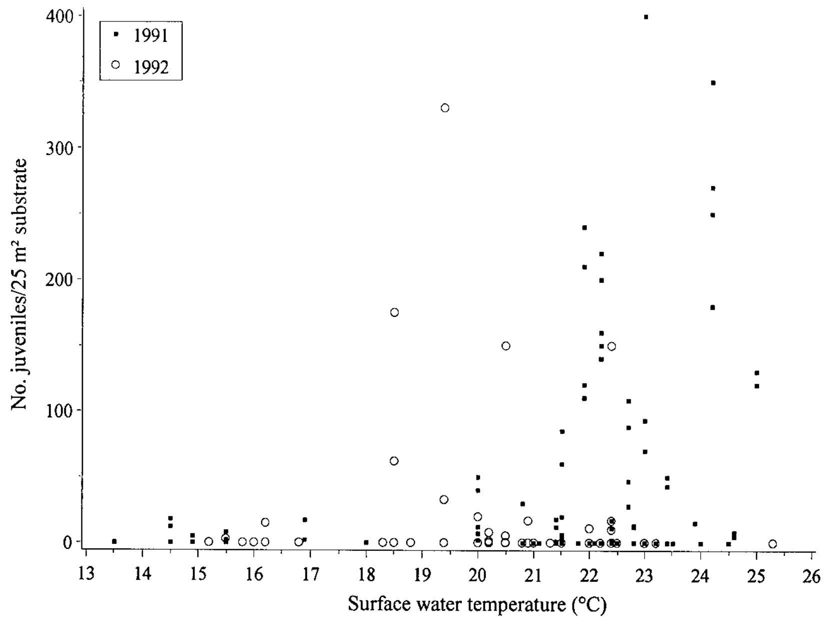
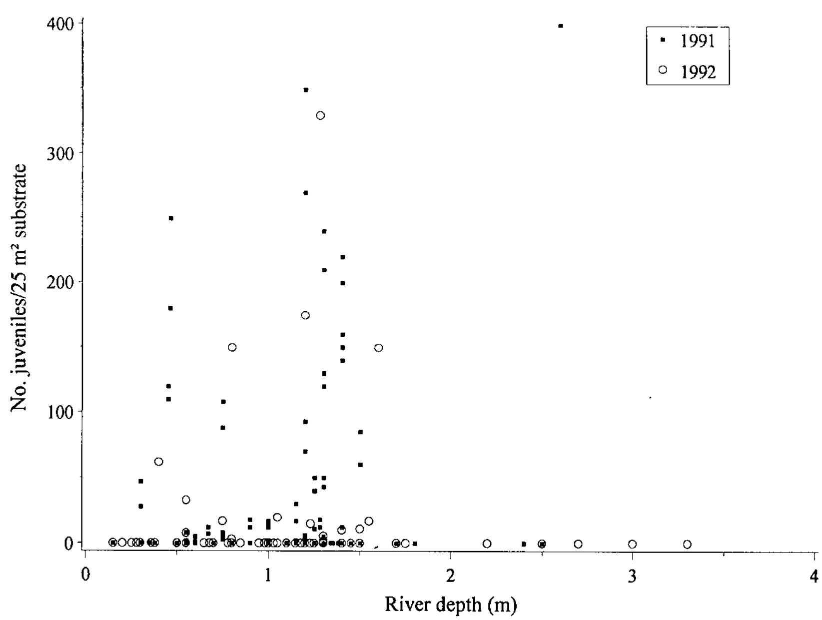


Fig. 21. Relation between juvenile American shad relative abundance and river depth in the upper Delaware River.



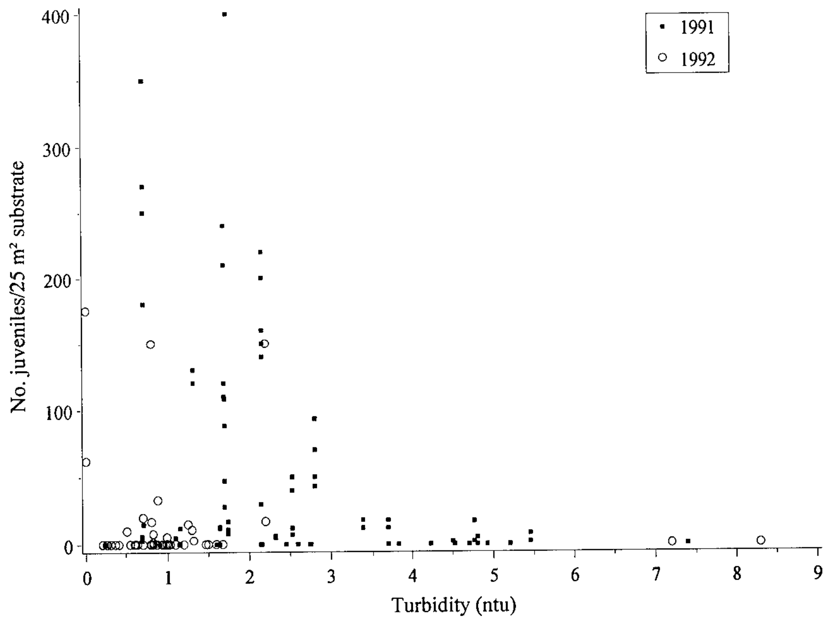


Fig. 22. Relation between juvenile American shad relative abundance and turbidity in the upper Delaware River.

spawning activity after 1900 h until 0100 h (Fig. 3) supports findings in numerous other studies (e.g., Massman 1952; Chittenden 1969). Current velocity (discussed below), river depth (greatest spawning activity at ≤1 m; Fig. 7), and turbidity (greatest spawning activity at ≤2 ntu; Fig. 8) may also affect spawning.

The HSI models for spawning adult American shad include two physical habitat variables, mean surface water temperature and mean water velocity during spawning season (Stier and Crance 1985). Superimposition of the water temperature model onto our data resulted in a good fit at the lower end of the distribution (Fig. 5); that is, nearly all the data fell within the SI curve. The data did not fit the model as well at the upper end of the distribution, however. We recommend extending the maximum-suitability limits to 24.5° C accordingly.

The results of regression analysis (Table 4; Fig. 6) and PCA (Fig. 4) did not agree for current velocity. In PCA an inverse relation to spawning

Table 13. *Linear (L) and quadratic (Q) relations detected from analysis of regression of six physical habitat variables on abundance of juvenile American shad by habitat type in the upper Delaware River. Relations listed are significant* (P < 0.05) *for both dive and seine-haul counts unless otherwise noted.*

	Habitat type					
Habitat variable	Channel[a]	Eddy	SAV[b]	Riffle	Riffle pool	Tributary
Temperature				L, Q		
Dissolved oxygen[a]						
River depth			L, Q			
Current velocity					L[c]	L, Q
Turbidity						L, Q
Percent SAV		L,[c] Q[c]	L, Q			

[a] There were no significant relations determined for either dissolved oxygen or channel categories.
[b] SAV = shallows having submerged aquatic vegetation.
[c] Dive counts only.

Table 14. *Comparison of dive-count abundance of juvenile American shad in six habitat types in the upper Delaware River.*

Habitat type	No. of counts[a]	Mean	Duncan group[b]
Eddy	17	42	A
Riffle pool	46	35	A
Channel	13	31	A
Riffle	46	22	A
Submerged aquatic vegetation	74	21	A
Tributary	12	16	A

[a] Each count = mean of three counts over a 5-m-square grid of substrate by a diver equipped with mask, fins, snorkel, and slate.
[b] ANOVA results: model DF 5, error DF 202, $F = 0.55$, $P = 0.74$.

activity was suggested, while regression showed no relation and a flat distribution to nearly 0.75 m/s (Fig. 6). Since American shad seemed to spawn as frequently in slow-moving water (0–0.3 m/s) as in moderate current velocities (0.3–0.75 m/s), these data essentially invalidate any lower suitability limit and indicate an upper maximum suitability limit of 0.7 m/s versus the 0.9 m/s limit of Stier and Crance (1985). Problems with the current-velocity model include scale and the possibility that single-point measurements of current velocity, even in habitats with slow or still waters, may not represent the entire current-velocity profile experienced by fish spawning there.

Though some spawning was observed in all habitat types examined, highest activity in runs and lowest in pools and riffle pools suggest some habitat selection by adult spawners. Physical attributes present in runs, partially characteristic of channels and SAV shallows, and absent from riffle pools and pools may explain such habitat preference. A combination of physical characteristics that seems to be avoided by spawning adults is slow current and greater depth. One or the other of these characteristics is present in the middle-ranked habitat types, but not both as a general observation. However, lowest-ranked habitat types are characterized by both deep and slow water. Perhaps either swift or shallow water (and especially both) confers higher survival to newly spawned eggs. Alternatively the observed habitat choice may be unrelated to physical variables and reflect some unknown ecological selective pressure, such as fewer egg predators in such habitats.

Eggs and Larvae

In interpreting the results of egg and larval physical-habitat data analysis, and in accordance with Rexstad et al. (1988), we place confidence in the methods of analysis as follows: regression analysis > PCA > range analysis. However, PCA-identified variables were rejected if regressions conflicted with the type of relation suggested by PCA. For habitat-type analysis, we place full confidence in the ANOVA and the further discrimination provided in the Duncan multiple range test. With these criteria, none of the physical habitat variables (exclusive of temporal factors and possibly sample depth) seem to be important correlates or determinants of American shad egg density. There was no significant effect of habitat type, which coincides with the nonmotile nature of the passively drifting eggs.

Prolarvae related strongly only to sample depth among physical variables and showed no ability to select habitat type. Postlarvae related strongly to sample and river depth as well as water temperature. They concentrated in riffle pools over other habitat types. Riffle pools, characterized by moderate depths and current variable in velocity and direction, may represent a refuge from drift or a better opportunity for larvae to forage and feed. Since sample depth was significant for all three life stages in regression, it suggests preferential habitat use of the deeper river zones regardless of river depth. Only water temperature for postlarvae stands out as an important remaining physical factor identified by both PCA and regression analysis.

The Stier and Crance (1985) HSI model for egg and larval stages of American shad includes only a single habitat variable, mean surface water temperature during the period when eggs and larvae are present. A minimum DO level of 5 mg/L (easily met in our study sites) and a maximum mean sediment concentration (midwater) of 100 ppm (not measured, but unlikely to be exceeded at any study location) were also specified. For evaluation of the model, egg and larval data from our study (only positive samples, i.e., where density >0) were superimposed on the SI graph for the same stages (Fig. 12). This comparison shows that, though some eggs were found below the thermal limit of the model (10° C) and at less than maximum suitability at

the upper thermal limits (26–27° C), moderate to high densities of eggs fell within the range of the model for maximum suitability (15–25° C). Prolarvae also fell within the range of maximum suitability except at the upper end, where moderate to high densities were found at >26° C (SI about 0.75). Postlarvae showed no reduction in density at the upper end of the thermal sampling range (26–27° C). These data indicate that the model needs to be modified for postlarvae, and possibly for prolarvae as well, to extend the suitability range to higher temperatures. Unfortunately, our data do not allow specification of the extent of change needed.

Our data also point to the importance of date in determining habitat suitability for egg and larval stages. This finding constitutes a seasonal effect related to other geographic variables such as latitude and river under study, as well as other habitat variables such as ambient water temperature. Our data (Fig. 9) indicate maximum suitability of 8 May to 18 June for eggs, 8 May to 17 June for prolarvae, and 14 May to 9 July for postlarvae on the upper Delaware River. Such suitability "windows" are clearly specific to river basins, even to river segments. The window limits are also subject to error because only three field seasons were used to determine them.

Time-of-day distributions for eggs and larvae were also noteworthy (Fig. 10). The distribution observed for eggs may result from a combination of three factors: (1) time of spawning, (2) specific gravity in water (slightly heavier than water), and (3) tendency of currents to carry suspended eggs for some distance (Massman 1952). The prolarval distribution could be explained by a vertical swimming response to light (–), although sampling error alone might be responsible. The vertical distributions depend greatly on the type of gear used to sample each life stage. Substrate sampling was not accomplished by our gear, for example.

The distributions of egg and larval stages with regard to current velocity, sample and river depth, and turbidity may also be described in terms of suitability indices. Such interpretations should not be construed as habitat requirements, however, because no causal relations have been demonstrated. All three life stages, for example, showed "maximum suitability" ranges in current velocity from 0.2 to 0.6 m/s (Fig. 13). Our data gave little, if any, indication of maximum suitability in either sample or river depth, however (Figs. 14 and 15). Nearly all points sampled in the water column at all river depths appeared suitable for all three life stages. Maximum suitability for turbidity seemed to range from 0.5 to 2.0 ntu (Fig. 16) for all three life stages.

Among the three life stages, only postlarvae showed significantly greater habitat use, and thus maximum suitability, for a particular habitat type, the riffle pool habitat. The only habitat type sampled where no eggs or larvae were obtained (zero suitability) was the shallow inshore SAV habitat.

Juveniles

Catchability of juvenile American shad by seines was relatively high (52–80%) in SAV habitats. These data compare to a mean of only 34% in similar habitat observed by Parsley et al. (1989). The methods used to determine catchability in SAV could not be used in other habitats because of high current velocities, deep waters, or heterogeneous substrates. Correlation analysis confirmed the propriety of using beach seines to quantify juvenile numbers in SAV habitats and indicated its justification in shallow riffle habitats also (Table 11). Because of relatively nonturbid water (90% of all observations at <3 ntu) with adequate underwater visibility (typically 3–5 m), underwater visual enumeration of juveniles on established quadrants was considered more reliable than seine-haul counts, especially in the case of a nonterritorial schooling species. Follow-up dive counts (10 min after initial counts) were consistent with initial counts.

The results of regression analyses were essentially the same whether dive or dive and seine data were used (Table 12). Since PCA revealed no or only weak relations to either physical variables or habitat types, conclusions regarding juvenile habitat use are based primarily on the regressions. The following habitat variables, in order, seemed to be important overall predictors of juvenile abundance: water temperature (+), river depth (+), turbidity (–), and DO (–).

When differentiated by habitat type (Table 13), however, juvenile abundance was affected by water temperature only in riffles. These results are difficult to explain on the basis of energetics because the warmer riffles, where juveniles were more abundant, would require a greater expenditure of energy for them to maintain position in the fast currents. If, however, the warmer waters hold sufficiently greater concentrations of planktonic or

drift food items, the energetic benefits may outweigh the costs.

River depth affected juvenile abundance primarily in SAV habitat, indicating that juveniles prefer the deeper SAV zones somewhat removed from shore and shallows. Turbidity was a factor (+) only in tributaries, where higher turbidities may have been associated with higher concentration of food items. Higher current velocities associated with the same habitat type may also have been related to food abundance. Percent SAV cover was found important only in SAV and eddy habitats (though SAV was present to lesser degrees in other habitat types), indicating that aquatic macrophytes provide forage-related advantage, cover, or some other resource in SAV and eddy habitats only. Since no effect of habitat type was observed on juvenile relative abundance at established quadrants, juvenile American shad seem to use all habitat types studied equally to their advantage. Thus, premigratory juveniles, in contrast to earlier life stages and spawning adults, may be habitat generalists.

Proposed HSI Models for Juveniles

We propose three HSI models, based on physical habitat variables, for premigratory juvenile American shad using nursery habitats in the Delaware River. The models as proposed are of preliminary nature because they are based on only two seasons of observation. They are also subject to modification by river basin, especially those based on or strongly affected by temporal variables (seasonal and time-zone effects). They are based on underwater dive counts only because of the uncertainty of seine efficiency in many habitat types.

Figures 20–22 show juvenile relative abundance at all study sites and habitats for water temperature, river depth, and turbidity. Dissolved oxygen is excluded because of its known lower limit for juveniles and strong relation to temperature. Maximum (1) and minimum (0) SI values, based on these scatter graphs, are listed in Table 15. Because most of the input variables to these models were shown to be habitat specific (Table 13), consideration should be given to the range and diversity of habitat types in the river system under study before applying the models. Further study is needed to determine upper and lower limits to the models where insufficient data precluded their specification.

The HSI models for American shad originally developed by Stier and Crance (1985) and modified or extended to include additional life stages by this study may be applied broadly to all river systems with caution. Our data indicate, however, that within a specific river basin, suitable ranges of physical factors for given life stages may be either broader or narrower than previously presumed. We also found that such suitability ranges can be habitat specific within river segments. These changes may be due to differences in food abundance, predators, or other unknown or unexamined biotic factors within specific habitats. If the range and proportion of habitat types in each river system of interest are known, HSI models for American shad may be applied cautiously on a comparative basis among river systems.

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Table 15. *Maximum (1) and minimum (0) suitability indices (SI) for juvenile American shad in nursery habitats for three habitat variables identified as predictors of relative abundance in the upper Delaware River. Missing values represent undetermined limits because of insufficient observations.*

Habitat variable	Lower-limit SI 0	Lower-limit SI 1	Upper-limit SI 1	Upper-limit SI 0
Water temperature (° C)	17	19.5	24.5	
River depth (m)	0.2	1.2		
Turbidity (ntu)	0.0	0.0	2.2	5.0

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